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Can we improve the nutritional quality of meat?

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The nutritional value of meat is an increasingly important factor influencing consumer preferences for poultry, red meat and processed meat products. Intramuscular fat content and composition, in addition to high quality protein, trace minerals and vitamins are important determinants of nutritional value. Fat content of meat at retail has decreased substantially over the past 40 years through advances in animal genetics, nutrition and management and changes in processing techniques. Evidence of the association between diet and the incidence of human non-communicable diseases has driven an interest in developing production systems for lowering total SFA and *trans* fatty acid (TFA) content and enrichment of *n*-3 PUFA concentrations in meat and meat products. Typically, poultry and pork has a lower fat content, containing higher PUFA and lower TFA concentrations than lamb or beef. Animal genetics, nutrition and maturity, coupled with their rumen microbiome, are the main factors influencing tissue lipid content and relative proportions of SFA, MUFA and PUFA. Altering the fatty acid (FA) profile of lamb and beef is determined to a large extent by extensive plant and microbial lipolysis and subsequent microbial biohydrogenation of dietary lipid in the rumen, and one of the major reasons explaining the differences in lipid composition of meat from monogastrics and ruminants. Nutritional strategies can be used to align the fat content and FA composition of poultry, pork, lamb and beef with Public Health Guidelines for lowering the social and economic burden of chronic disease.

Meat lipid composition: Nutrition and genetics: Product quality: Human health: Rumen lipid metabolism

Data from clinical trials, controlled metabolic interventions and prospective cohort studies indicate that the substitution of SFA and *trans* fatty acids (TFA) for PUFA lowers mortality and markers of CVD risk[1–5]. Most public health policies in developed countries recommend population wide decreases in the consumption of SFA and TFA and an increase in PUFA intake to lower the incidence of CVD and metabolic diseases[6–8]. Despite the establishment of nutritional guidelines, dietary surveys indicate that the intakes of SFA typically exceed recommended levels, while the consumption of PUFA, specifically *n*-3 PUFA is often below the optimal range[9–12]. The majority of PUFA in the human diet originates from plant oils and vegetable fats containing relatively high proportions of linoleic acid (18 : 2 *n*-6) and linolenic acid (18 : 2 *n*-3), while intakes of the long chain *n*-3 PUFA, EPA (20 : 5 *n*-3) and DHA (22 : 6 *n*-3) contained in oily fish fall short of a recommended target of 450 mg/d[13].

In most developed countries, meat and meat products are a significant source of fat and SFA in the human diet, but also contribute to 20 : 5 *n*-3, docosapentaenoic acid (22 : 5 *n*-3) and 22 : 6 *n*-3 consumption[9–13]. Ruminant-derived meat and meat products are also a source of TFA in the human diet[14–17]. Altering the fat content and fatty acid (FA) composition of meat and meat products offers the opportunity to realign the consumption of FA in human populations closer to Public Health guidelines for lowering the incidence of non-

Abbreviations: CLA, conjugated linoleic acid; FA, fatty acid; IMF, intramuscular fat; TFA, *trans* fatty acids.

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communicable diseases without requiring substantive changes in consumer eating habits. Global meat consumption is projected to increase within the next 30 years[18], highlighting that the potential benefits and impact from altering the fat content and FA composition of poultry, pork, beef and lamb will become increasingly important. The present paper focuses on approaches to improving the lipid composition of meat. The impact on aspects of meat quality including colour, shelf life and sensory were recently reviewed[19] and hence not considered in the present manuscript.

Lipid in meat from monogastric and ruminant animals

Lipid content of meat varies depending on muscle and tissue type, animal species and production system that affect nutritional, sensory and technological properties and overall quality[14,20]. Furthermore, FA composition determines the physical and textural properties of adipose and the oxidative stability of muscle, which affects flavour, juiciness, tenderness, muscle colour and overall liking. Fat in meat is deposited in intramuscular, intermuscular and subcutaneous adipose stores mainly in the form of glycerol esters, cholesterol, phospholipids and FA esters. Intramuscular fat (IMF) content of chicken, pork, beef and lamb typically varies between 10–25, 15–40, 20–50 and 30–80 g/kg, respectively[14,15,20,21]. For chicken, the lipid content of dark meat and light meat averages 28 and 11 g/kg, respectively[21–26]. The IMF of chicken and pork contains 260–350, 290–460 and up to 200 g/100 g, as SFA, MUFA and PUFA, respectively[21–33]. In beef and lamb, IMF contains 450–480 and 350–450 g/100 g of SFA and MUFA, respectively and up to 50 g/100 g as PUFA, respectively [17,18]. The ratio of PUFA:SFA in IMF of beef or lamb is typically low at about 0·1–0·2 except for very lean animals (<10 g/kg IMF) or animals fed rumen protected lipid supplements where this ratio can be as high as 0·5–0·7[14,15]. The ratio of *n*-6:*n*-3 PUFA in ruminant meat (abundance of α-linolenic acid (18 : 3 *n*-3), and to a lesser extent 22 : 5 *n*-3 and 22 : 6 *n*-3, relative to 18 : 2 *n*-6 and arachidonic acid (20 : 4 *n*-6)) from pasture or diets based on grass or forage legume silages is generally <3·0, but this ratio can exceed 5·5 in animals fed high amounts of cereal grains[14,15].

Lipid in beef, lamb and other ruminant meat products also contain isomers of conjugated linoleic acid (CLA) and TFA. Depending on muscle type, production system and breed the proportions of total CLA and TFA in retail beef vary between 0·34–0·82 and 2·97–5·63 g/100 g total FA, respectively, corresponding to between 9·8–98 and 70–586 mg/100 g muscle[34–36]. Measurements for retail lamb are limited, but a recent report indicated that the proportions of total CLA and TFA accounted for 0·59–1·44 and 6·41–12·0 g/100 g FA[37].

Nutritional approaches to enhance fatty acid composition

Diet is known to influence the FA composition of meat and meat products. Numerous investigations have examined the potential to: (i) lower the relative proportions of SFA, (ii) increase the overall PUFA:SFA ratio and (iii) enrich *n*-3 PUFA relative to *n*-6 PUFA in intramuscular lipid. In ruminants, increases in specific FA, including *cis*-9, *trans*-11 CLA have been targeted. Most studies have focused on including oilseeds, plant oils, fish oils, marine algae in the diet of pigs[27–33], poultry[22,23,24–26], cattle[38–41] and sheep[42–45] to alter meat FA composition and content. In ruminants, the use of lipid supplements protected from ruminal metabolism have also been investigated[14,15,46,47]. Both the processes of digestion and metabolism of absorbed lipid in the host animal have a major impact on the transfer efficiency of dietary FA into meat. In monogastric animals, the small intestine is the major site for the digestion of dietary lipid. Digestion involves the action of pancreatic lipase to hydrolyse TAG into 2-monoacylglycerol and free acids and the formation of micelles followed by absorption in the intestinal mucosa and transport of FA in the peripheral circulation for uptake by body tissues mediated by lipoprotein lipase[48]. In pigs and poultry, dietary lipid remains largely intact before absorption and incorporation into tissue lipid, and therefore changes in dietary FA intake have a largely predictable influence on tissue lipid composition. Digestion of dietary lipid in ruminants is far more complicated due to the metabolic activity of the microbial community in the rumen-reticulum. As a result, meat from ruminant animals, such as beef and lamb, contains a more diverse range of FA that bear little resemblance to the composition and amount of FA supplied by the diet[49]. Dietary unsaturated FA, PUFA in particular, have toxic effects on certain rumen microorganisms[50,51]. To alleviate the inhibitory effects on growth, the rumen microbiome has evolved to secrete proteins capable of hydrolysing ester bonds of esterified FA and decreasing the degree of unsaturation of the free FA released through reduction, isomerisation or hydration. Lipolysis and biohydrogenation result in extensive metabolism of dietary PUFA to saturated end-products limiting the escape of dietary PUFA from the rumen. However, biohydrogenation is incomplete, resulting in the formation of FA intermediates often containing one or more *trans* double bonds[16,52], which following absorption are used as substrates for tissue lipogenesis. Understanding the mechanisms responsible and microbiota and their associated enzymes capable of these reactions is central to future attempts to develop nutritional strategies for strategic and more predictable changes in the FA composition of ruminant meat.

Potential for reengineering ruminal lipid metabolism

Understanding of the role of rumen bacteria in biohydrogenation has traditionally been based on investigations with bacteria able to be cultured *ex vivo*. Culturable *Butyrivibrio* spp. capable of biohydrogenation have been the most widely studied. However, development of new molecular methods have enabled more informed investigations of rumen microbiome–lipidome

interactions[52–55] based on experiments involving the use of dietary lipid supplements to alter ruminal lipid metabolism and application of next generation sequencing technologies to characterise the impact on the metataxonome. Changes in the ruminal bacterial taxa have highlighted that the communities involved in biohydrogenation are potentially much more diverse than implicated from historical studies with pure cultures[54–56] that are now known to include *Prevotella*, *Lachnospiraceae incertae sedis* and unclassified *Bacteroidales*, *Clostridiales*, *Succinovibrio*, *Roseburia* and *Ruminococcaceae*, species identified as yet unculturable. Such findings highlight the challenges to developing targeted approaches for altering the biohydrogenation activity of the rumen microbiota.

Much less is known about the microbiology underpinning lipolysis of esterified lipid in the rumen. Few culturable isolates with known lipolytic activity have been identified, and historically only bacterial genera, namely *Anaerovibrio lipolyticus* and *Butyrivibrio* spp. have been shown to have lipolytic capacity, with *A. lipolyticus* being specific to TAG and *Butyrivibrio* being specific towards phospholipids. Nonetheless, the lipases possessed by these bacteria and others within the rumen microbiome have until recently remained relatively understudied. Recently, the creation of rumen bacterial fosmid-based metagenomic libraries, enabled twelve lipase/esterase genes and two phospholipases to be isolated, the sequences of which appear to originate from bacteria that cannot as yet be cultured *ex vivo*[55]. A draft genome of *A. lipolyticus* coupled with annotation and biochemical characterisation also allowed the characterisation of three identified lipases with activity against TAG[57]. This new knowledge will be invaluable to understanding the biological potential to alter the extent of lipolysis in the host ruminant in the future.

Both bacteria and protozoa leaving the rumen are also an important source of FA available for absorption by the host animal. Membrane lipids of rumen bacteria contain relatively high proportions of odd-chain and branched-chain FA. Rumen protozoa are relatively rich in MUFA, PUFA and isomers of CLA, possibly due to engulfment of chloroplasts that contain the majority of 18 : 3 *n*-3 in structural components of plant thylakoid membranes[58–60]. Intra-protozoal chloroplast lipid metabolism may also facilitate the direct uptake of the major FA in chloroplasts (16 : 0, 18 : 2 *n*-6 and 18 : 3 *n*-3) into protozoal membranes. Furthermore, co-localisation of chloroplasts and engulfed bacteria within food vacuoles may also lead to intra-protozoal lipolysis and the biohydrogenation of PUFA in ingested chloroplasts, assuming that co-localised bacteria exhibit lipolytic and biohydrogenation activity. Such a mechanism may explain the rather high proportion of CLA isomers in the lipid of rumen protozoa. Nevertheless, increases in intra-protozoal chloroplast content do not appear to increase ruminal escape of PUFA[59]. Zero grazing of growing steers was found to elevate intra-protozoal chloroplast content compared with a semi-synthetic diet based on straw and concentrates, but the amount of PUFA reaching the duodenum did not differ between dietary treatments as the protozoal flow from the rumen to the duodenum was low following zero grazing. It is hypothesised that perhaps the higher sugar content of grass and subsequent chemotaxis of protozoa towards sugars may enhance their likelihood of remaining within the rumen. Future investigations are required to establish whether it is possible to simultaneously increase the PUFA content of protozoa and increase outflow of PUFA-enriched protozoa from the rumen.

Dietary sources of PUFA

While forages are rarely used to support the nutritional requirements of monogastric animals, these represent important feed resources for ruminants. It is well established that diets based on fresh or conserved forages typically result in higher *n*-3 PUFA and lower *n*-6 PUFA content of lamb and beef compared with cereals[14,15,61–65]. Even though forage has a relatively low lipid content, varying between 30 and 100 g/kg DM, it is a rich source of PUFA, particularly 18 : 3 *n*-3, which accounts for 50–75% of total forage FA content in grasses and forage legumes[58,66]. Depending on production system, forages are often the primary source of FA in the ruminant diet[58,67], which in addition to being relatively inexpensive and a sustainable feed resource, underpins an expanding market for 'grass-fed' or 'grass-finished' ruminant meat products with a lower total fat and increased *n*-3 PUFA content[68–70]. Both environment and genetics influence FA biosynthesis and forage lipid content[69,71,72], highlighting the potential to select for grasses with a higher lipid content to increase PUFA intakes in the host ruminant. Several secondary metabolites in plants have been suggested to afford some protection of forage PUFA from lipolysis and biohydrogenation in the rumen. Many of these compounds are associated with a variety of 'weed' species common in species-rich pasture[69] that include condensed tannins[73,74], saponins[75,76], catecholamines[77] and essential oils[76].

Oilseeds are rich in C_{18} unsaturated FA, but differ in relative abundance of oleic acid (*cis*-9 18 : 1), 18 : 2 *n*-6 and 18 : 3 *n*-3, which have been used to alter the FA composition of poultry meat and pork. Rapeseed is rich in *cis*-9 18 : 1, sunflower and safflower contain high proportions of 18 : 2 *n*-6, while linseed, flaxseed and camelina are common sources of 18 : 3 *n*-3. Use of dietary supplements of linseeds and linseed oil have been the most widely investigated for enriching *n*-3 PUFA in meat from chickens, pigs and ruminants. In addition to elevating 18 : 3 *n*-3 concentrations, the abundance of 20 : 5 *n*-3, 22 : 5 *n*-3 and 22 : 6 *n*-3 in intramuscular lipid is often increased[63,67,78,79] due to the elongation and desaturation of 18 : 3 *n*-3.

Fish oil and marine algae are the richest available sources of 20 : 5 *n*-3, 22 : 5 *n*-3 and 22 : 6 *n*-3 and have been used as dietary supplements to increase the long chain *n*-3 PUFA content of meat. In pigs and chickens the extent of long-chain *n*-3 PUFA enrichment is determined by the level of supplementation[22,25,30]. Despite

extensive metabolism of 20 : 5 *n*-3, 22 : 5 *n*-3 and 22 : 6 *n*-3 in the rumen[52,80,81], marine lipid supplements can be used to increase the long-chain *n*-3 PUFA content of beef and lamb[40,42,44,45]. However, both fish oil and marine algae also inhibit the complete biohydrogenation of C_{16} and C_{18} unsaturated FA in the rumen causing numerous *trans* mono- and polyenoic intermediates to accumulate and a decrease in 18 : 0 formation[56,80–84], changes that lead to an increase in the TFA content of beef[40] or lamb[42,44,45].

Specialised lipid supplements have been developed to be more resistant to lipolysis and biohydrogenation in the rumen to increase the amount of PUFA available for deposition, elongation and desaturation in muscle and adipose tissue. Protected lipid also minimise the adverse effects of lipid on ruminal digestion and can be used to increase the amount of fat in the earlier recommended ruminant diet levels (<60 g/kg diet DM). Various technologies have been developed in an attempt to protect plant or marine lipid sources from lipolysis and biohydrogenation in the rumen, that include encapsulating oils with a protein matrix and treating with formaldehyde; feeding lipid as calcium soaps or FA amides; physical processing of oilseeds (heating, grinding, cracking, bruising, rolling, extruding) or whole intact oilseeds[19,46,85]. However, the potential to increase the outflow of PUFA from the rumen using these supplements is often rather limited, and known to vary depending on the method used and source of protected lipid[85]. Inevitably, the use of protected supplements also increase the cost of ruminant meat production that would need to be recovered by a premium at retail[19].

Enrichment of PUFA in meat from monogastrics

Two main approaches have been used to increase the *n*-3 PUFA content of pork and chicken that include dietary supplements of linseed or flaxseed as a source of 18 : 3 *n*-3, and the use of fish oil or marine algae as a source of 20 : 5 *n*-3 and/or 22 : 6 *n*-3 and demonstrated the potential to enrich the *n*-3 PUFA content of intramuscular lipid in growing pigs and chickens (Tables 1 and 2, respectively). Dietary supplements of oilseeds can be used to increase in the 18 : 3 *n*-3 content of muscle in pigs [27–29,31–33]. Even though *cis*-9 18 : 1 is the major FA in rapeseed and olive oil, these lipid can be used to elevate 18 : 3 *n*-3 in pork, but to a much lesser extent than linseed or flaxseed (Table 1). Enrichment of 18 : 3 *n*-3 in body tissues of growing pigs is determined by the amount of flaxseed in the diet[32]. Supplements of flaxseed (50 g/kg diet) resulted in a 5-fold increase in 18 : 3 *n*-3 content relative to the control diet, while higher inclusion rates (100 g flaxseed/kg diet) resulted in a 15-fold enrichment of 18 : 3 *n*-3 than the control. Dietary supplements of marine algae have also been shown to result in dose dependent increases in 22 : 6 *n*-3 content of bacon[30]. Enrichment of 20 : 5 *n*-3, 22 : 5 *n*-3 and 22 : 6 *n*-3 was higher for pigs fed diets containing algae at 16 g/kg compared with 6 g/kg. The potential of using a mixture of linseeds and fish oil to alter the *n*-3 PUFA content of pork has also been investigated[28]. Linseed supplementation increased 18 : 3 *n*-3 content and enriched 20 : 5 *n*-3, 22 : 5 *n*-3 and 22 : 6 *n*-3 due to elongation and desaturation of 18 : 3 *n*-3 in body tissues. Much higher increases in 20 : 5 *n*-3, 22 : 5 *n*-3 and 22 : 6 *n*-3 content were achieved in growing pigs fed diets containing fish oil with minimal effects on the proportion of 18 : 3 *n*-3 in total lipid.

Similar investigations have been made in chickens (Table 2). Access to pasture or chicory plus a control basal diet was found to alter the FA content of chicken breasts compared with a diet containing linseed and high *cis*-9 18 : 1 sunflower seed[23]. Muscle from chickens fed the control plus chicory diet contained higher amounts of *n*-6 and *n*-3 PUFA than the control plus pasture diet due to increases in total fat content. Treatments had no effect on FA other than increasing 20 : 5 *n*-3 abundance. Substituting the control diet for the diet containing linseed and sunflower seed in growing chickens offered access to pasture, decreased total *n*-6 PUFA and elevated total *n*-3 PUFA content, including 20 : 5 *n*-3, 22 : 5 *n*-3 and 22 : 6 *n*-3. However, similar changes in muscle FA composition were not observed when birds had access to chicory. Enrichment of 18 : 3 *n*-3, 20 : 5 *n*-3, 22 : 5 *n*-3 and 22 : 6 *n*-3 in breast meat from chickens fed diets containing flaxseed also increases with time on diet[26]. Long chain *n*-3 PUFA content of chicken can also be elevated in birds fed diets containing fish oil and marine algae up to 210 mg/100 g[24,25].

Enrichment of PUFA in meat from ruminants

Despite extensive lipolysis and biohydrogenation of lipid in the rumen by the rumen microbiome, diet is the major environmental factor influencing the FA composition of ruminant meat. Forage is an important component in most ruminant diets and can be used to influence the FA composition of beef and lamb. The IMF content and FA composition of beef differs between animals finished on grass or fed concentrates[64,65]. Grass-finished beef typically contains higher amounts of 18 : 3 *n*-3 (Table 3). Depending on management system, 20 : 5 *n*-3, 22 : 5 *n*-3 and 22 : 6 *n*-3 content is also elevated due to the elongation and desaturation of 18 : 3 *n*-3 in body tissues. Even for animals reared on pasture, feeding concentrates during the finishing period causes depletion of 18 : 3 *n*-3 and higher accretion of 18 : 2 *n*-6[64,65]. Similar changes in the FA composition of IMF also occur in growing lambs (Table 4). Forages can be used to lower total and saturated fat content and increase the *n*-3 PUFA content relative to cereal-based diets[19,68–70].

Dietary plant and marine lipid supplements can be used to alter the FA composition of beef (Table 3) and lamb (Table 4). Flaxseed supplementation of a fresh forage basal diet was found to have no effect on *n*-6 and *n*-3 PUFA in beef, but the content of *trans*-11 18 : 1 and *cis*-9, *trans*-11 CLA was higher for animals finished on fresh forage compared with a diet containing flaxseed[41]. Furthermore, flaxseed supplements also increased

Table 1. Effect of dietary lipid supplements on the PUFA content of pork (mg/100 g)

Reference	Breed	Sex	Supplement	Inclusion (g/kg)	Time (d)	Age (d)	Wt. (kg)	Muscle	*n*-6 PUFA		*n*-3 PUFA				Total FA
									18 : 2	20 : 4	18 : 3	20 : 5	22 : 5	22 : 6	
Oilseeds															
Bertol *et al.*[31]	D/E/M	M/F (50:50)	Soyabean oil	30	42	173	111	*L. dorsi*	245·7	43·1	20·5	NR	NR	NR	1770
			Rapeseed oil	30	42	172	112		224·1	44·6	24·2	NR	NR	NR	1940
			Rapeseed oil: Flaxseed oil (1:1)	30	42	172	113		238·0	39·1	43·9	NR	NR	NR	2080
Gjerlaug-Enger *et al.*[33]	D × [Y × LR]	M + F	Control*	0	NR	NR	83	*L. dorsi*	224·2	62·1	9·5	8·2	15·8	10·5	1900
			Rapeseed expeller + rapeseeds	130 + 56	NR	NR	82		222·7	51·0	20·6	11·4	17·5	8·2	1700
Guillevic *et al.*[29]	P × [LR × LW]	M	Palm and sunflower oil (1:1)	16	NR	NR	107	*L. dorsi*	1,006	53·1	56·6	3·5	10·4	5·2	8700
			Extruded linseeds	42	NR	NR	108		1,108	59·5	399·4	11·5	25·9	5·8	9600
Nuernberg *et al.*[27]	P × German LR	M/F (50:50)	Olive oil	50	NR	NR	106	*L. dorsi*	139·3	57·4	9·2	2·0	7·3	1·2	1450
			Linseed oil	50	NR	NR	106		179·5	31·8	126·6	24·4	20·2	0·5	1450
Turner *et al.*[32]	CP × Line C337	M/F (50:50)	Control*	0	76	–	124	*L. dorsi*	422·0	59·8	41·0	5·3	15·4	6·4	6141
			Extruded flaxseed	50	76	–	120		498·0	49·5	237·0	20·4	33·2	9·3	5174
			Extruded flaxseed	100	76	–	121		653·0	34·3	615·0	31·9	39·6	8·1	5788
Marine															
Haak *et al.*[28]	Topigs 40 × P	M + F	Control	0	98–109	–	–	*L. thoracis*	154·6	40·0	7·6	3·0	6·5	1·9	1380
			Linseed	30	98–109	–	–		155·0	35·5	18·5	8·1	11·2	2·7	1490
			Fish oil	12	98–109	–	–		158·2	29·5	8·4	24·5	14·7	18·3	1790
Meadus *et al.*[30]	D × LW	M	Marine algae	0·6	25	–	108	Belly	298·6	12·6	57·0	1·4	1·4	4·3	2882
			Marine algae	6	25	–	113		306·5	13·0	58·4	1·8	3·6	12·2	3110
			Marine algae	16	25	–	112		352·9	14·8	66·6	3·6	9·7	33·9	3325

D, Duroc; E, Embapa; Y, Yorkshire; LR Landrace; P, Pietrain; LW, Large White; CP, Camborough Plus., M, Moura, NR, not reported.
* Control diet contained animal fat that was completely or partially replaced with test lipid supplements.

Table 2. Effect of diet on the fatty acid (FA) content of chicken breast (mg/100 g)

Reference	Breed	Sex	Diet/supplement	Inclusion (g/kg)	Time (d)	Age (d)	*n*-6 PUFA		*n*-3 PUFA				Total FA
							18 : 2	20 : 4	18 : 3	20 : 5	22 : 5	22 : 6	
Forage													
Azcona *et al.*[23]	Camperos	ND	Control (Confined)	–	45	85	185·4	55·3	16·3	1·2	7·5	7·1	950
			Control + Pasture	–	45	85	181·1	49·1	14·0	2·3	5·5	7·3	840
			Linseed + Pasture + SS	55	45	85	167·3	40·1	39·7	5·4	11·2	13·3	920
			Control + Chicory	–	45	85	248·2	55·6	23·3	5·8	8·0	9·4	1230
			Linseed + Chicory + SS	55	45	85	114·5	43·8	16·2	2·9	9·0	9·0	700
Oilseeds													
Mirshekar *et al.*[26]	Cobb 500	ND	Soyabean oil*	(25)/50	(21)/21	42	704·0	18·0	157·0	17·0	NR	15·0	3150
			Flaxseed oil	50	7	42	833·0	34·0	201·0	20·0	NR	22·0	3241
			Flaxseed oil	50	14	42	874·0	37·0	213·0	33·0	NR	30·0	3233
			Flaxseed oil	50	21	42	932·0	67·0	236·0	47·0	NR	45·0	3211
			Flaxseed oil*	(25)/50	(7)/21	42	1,011·0	66·0	293·0	48·0	NR	48·0	3234
			Flaxseed oil*	(25)/50	(14)/21	42	1,001·0	75·0	391·0	52·0	NR	52·0	3266
			Flaxseed oil*	(25)/50	(21)/21	42	811·0	76·0	432·0	58·0	NR	59·0	3260
Marine													
Cortinas *et al.*[22]	Ross	F	Tallow	90		44	199·0	41·0	18·0	3·0	NR	10·0	1885
			Tallow:Linseed oil:Fish oil	55/30/5		44	228·0	28·0	189·0	30·0	NR	40·0	1833
			Tallow/Linseed oil/Fish oil	35/45/10		44	229·0	23·0	249·0	40·0	NR	42·0	1701
			Linseed oil/Fish oil	70/20		44	282·0	22·0	410·0	57·0	NR	48·0	1809
Kalogeropoulos *et al.*[24]	ND	ND	Control	0	NR	5–554	537·6	85·8	38·4	11·6	22·3	22·8	2510
			Microalgae	23 g†	NR	45–55	297·5	65·2	15·1	12·0	19·5	85·0	1710
Rymer *et al.*[25]	Ross 308	ND	Control‡	–	21	42	335·0	73·0	27·0	4·0	15·0	24·0	1146§
			Fish oil	44	21	42	174·0	26·0	11·0	31·0	46·0	129·0	1122§
			Encapsulated fish oil	26	21	42	257·0	36·0	20·0	18·0	27·0	122·0	1119§
			Marine algae	11	21	42	276·0	51·0	22·0	9·0	19·0	111·0	1146§
			Marine algae	22	21	42	325·0	52·0	27·0	6·0	16·0	147·0	1348§
			Marine algae	33	21	42	266·0	50·0	20·0	9·0	14·0	187·0	1237§

ND, not determined; NR, not reported; SS, high oleic acid sunflower seeds.
* Values in parenthesis indicate the amount of oil in the starter diet fed until 21 d of age before switching to the grower diet fed for 21 d before slaughter.
† Birds received 23 g/lifetime of dried marine microalgae containing 180 g of 22 : 6 *n*-3/kg.
‡ Control diet contained 50 g/kg of blended vegetable fat that was partially replaced with test lipid supplements.
§ Calculated as the sum of all reported fatty acids.

Table 3. Effect of diet on the fatty acid (FA) composition of beef (mg/100 g)

Reference	Breed	Sex	Diet/supplement	Inclusion rate	Age (m)	Wt (kg)	Muscle	*n*-6 PUFA		*n*-3 PUFA				Total FA
								18 : 2	20 : 4	18 : 3	20 : 5	22 : 5	22 : 6	
Forage														
Ponnampalam *et al.*[64]	Mixed (SH, HE)	–	Grass-finished	–	18	NR	*L. dorsi*	108·8	59·6	32·4	24·5	36·5	4·2	2120
			Grain-finished (80 d)	–				118·8	37·6	10·3	11·1	23·6	3·7	1538
			Grain-finished (150–200 d)	–				167·4	58·5	14·9	13·1	31·6	3·7	3614
Aldai *et al.*[65]	Asturiana de los Valles	M	Pasture	–	12	NR	*L. dorsi*	76·5	17·8	18·2	5·6	7·1	0·5	547
			Pasture + 1 m Concentrate	–				95·3	26·0	16·3	7·5	9·3	0·6	813
			Pasture + 2 m Concentrate	–				103·3	24·8	12·5	7·7	9·4	0·8	1055
Oilseeds														
Pouzo *et al.*[41]	AA	M	Control (Pasture)	–	–	487	*L. dorsi*	72·6	34·0	25·8	14·7	20·6	3·3	3272
			Pasture + maize grain	–		490		92·2	40·0	24·3	14·6	22·6	3·1	3478
			Pasture + maize grain + Flaxseed	1·25 g/kg LW		494		86·2	32·9	26·9	13·6	20·6	3·2	3168
			Pasture + maize grain + Flaxseed	2·50 g/kg LW		494		75·7	33·3	26·7	14·6	20·1	2·9	2868
Kim *et al.*[38]	CHX	M	Control – Grass Silage	–	NR	NR	*L. dorsi*	47·1	NR	28·6	16·7	NR	3·3	3179
			Echium oil (1·5%)	15 g/kg DM				52·4	NR	31·3	15·5	NR	3·3	4090
			Echium oil (3·0%)	30 g/kg DM				54·2	NR	32·1	14·5	NR	2·7	4075
			Linseed oil (3·0%)	30 g/kg DM				50·0	NR	30·6	17·0	NR	3·4	3385
Nassu *et al.*[39]	British × Continental	F	Grass hay	–	NR	NR	*L. thoracis*	147·7	47·7	29·0	13·6	25·0	NR	5680
			Grass hay + Flaxseed	141 g/kg				141·0	32·9	71·7	15·9	23·5	NR	5875
			Barley silage	–				142·2	42·7	21·0	8·8	20·3	NR	6772
			Barley silage + Flaxseed	87·1 g/kg				136·0	34·0	68·0	14·7	23·1	NR	6413
Marine														
Angulo *et al.*[40]	German Holstein	F	Control*	–	NR	NR	*L. dorsi*	81·0	32·9	17·5	8·8	17·5	1·3	2191
			Linseed oil + Marine algae	27 + 4 g/kg DM				89·0	24·9	35·6	10·7	14·2	10·7	3558
			Sunflower oil + Marine algae	27 + 4 g/kg DM				112·2	26·4	19·8	9·9	13·2	13·2	3301
Dunne *et al.*[47]	Continental crossbred	F	Control†		NR	NR	*L. thoracis*	80·4	NR	13·3	13·0	NR	3·4	2870
			Rumen protected fish oil	275 g/d				82·0	NR	27·9	52·3	NR	15·4	3890

NR, not reported; SH, Shorthorn; HE, Hereford; AA, Aberdeen Angus; CHX, Charolais cross.
* Control diet contained 31 g/kg diet DM of saturated fat sources that replaced with test lipid supplements.
†Control diet contained a prilled fat rich in 16 : 0 that was partially replaced with a rumen protected source of fish oil.

Table 4. Effect of diet on the fatty acid (FA) content of lamb (mg/100 g)

Reference	Breed	Sex	Diet/supplement	Inclusion rate	Age (m)	Wt (kg)	Muscle/tissue	*n*-6 PUFA		*n*-3 PUFA				Total FA
								18 : 2	20 : 4	18 : 3	20 : 5	22 : 5	22 : 6	
Forage														
Fisher *et al.*[61]	S × Mule	M	Grass	–	–	–	Topside	119·0	45·0	41·0	24·0	27·0	10·0	1853
			Concentrate	–				188·0	62·0	14·0	8·4	16·0	5·5	1963
Díaz *et al.*[62]	RA	ND	Concentrates + Straw (Spain)	–	–	–	*L. dorsi*	154·6	63·2	9·7	5·7	11·1	4·1	1662
	S/SCH × ML		Grass + Concentrate (Germany)	–			(Retail)	152·3	33·9	42·1	14·5	16·2	5·9	2808
	British		Grass + Concentrate (UK)	–				91·4	25·6	39·6	21·9	18·8	5·3	2431
	C		Grass (Uruguay light)	–				94·4	28·1	54·0	18·9	17·0	4·5	1683
			Grass (Uruguay heavy)	–				158·0	31·2	125·5	32·2	22·2	6·2	3908
Oilseeds														
Noci *et al.*[43]	S crossbred	M	Ca-salts of palm oil distillate*	60 g/kg DM	–	57	*L. dorsi*†	121·6	21·1	17·6	2·5	7·0	1·4	3524
			Camelina oil	60 g/kg DM		57		133·2	15·4	59·2	5·1	9·3	2·3	4659
			Linseed oil	60 g/kg DM		57		125·7	12·9	72·7	5·0	8·8	1·3	4177
			Protected Camelina seed	60 g/kg DM		57		122·1	14·6	67·3	6·5	8·9	1·6	4056
			Protected Linseed	60 g/kg DM		56		120·6	16·7	101·9	11·9	12·7	3·2	3980
			Protected Camelina oil	60 g/kg DM		58		138·5	12·1	79·2	5·0	8·3	1·3	4171
Marine														
Hopkins et al[44]	PD × BL × M	M	Silage (Dam) + Control	–	–	–	*L. dorsi*	297·0	104·0	39·0	30·0	38·0	13·0	4989‡
			Silage (Dam) + Microalgae	19·2 g/kg DM				305·0	104·0	39·0	48·0	37·0	92·0	4976‡
			Concentrate (Dam) + Control	–	–	–	*L. dorsi*	290·0	101·0	41·0	29·0	37·0	12·0	5061‡
			Concentrate (Dam) + Microalgae	19·2 g/kg DM				295·0	99·0	37·0	44·0	34·0	71·0	4,859‡
Meale *et al.*[45]	CA	M + F	Control	–	–	>45	Skirt	605·0	–	36·5	8·4	29·0	9·0	NR
			Microalgae	10 g/kg DM				418·0	–	27·5	9·1	40·1	50·0	NR
			Microalgae	20 g/kg DM				398·0	–	24·6	17·9	46·1	58·0	NR
			Microalgae	30 g/kg DM				451·0	–	24·9	32·1	61·3	114·0	NR
Annett *et al.*[42]	Mixed commercial	M	Grass	–	70	47	L. dorsi	92·4	10·1	38·2	10·5	4·6	8·0	4200
			Grass + Concentrate	–	68	47		96·9	5·6	45·4	4·6	3·1	5·6	5100
			Grass + Concentrate + Fish oil	14 g/d	68	47		175·5	20·8	54·6	11·7	6·5	5·9	6500
			Concentrate	–	53	44		240·8	3·9	38·1	11·8	8·4	1·7	5600
			Concentrate + Fish oil	14 g/d	58	44		188·8	5·3	20·7	24·8	28·9	27·7	5900

ND, not determined; NR, not reported; S, Suffolk; RA, Rasa Aragonesa; SCH, Schwarzkopfe; ML, Merino Landschaf; C, Corriedales; PD, Poll Dorset; BL, Border Leicester; M, Merino; CA, Canadian Arcott.
* Composition of intramuscular lipid.
† All treatments were fed for 100 d.
‡ Calculated as the sum of all reported fatty acids.

subcutaneous fat thickness compared with grazing animals. The potential of flaxseed supplementation to alter IMF composition has also been assessed in growing cattle fed a basal diet based on grass-hay or barley-silage[39]. For both diets, flaxseed lowered 18 : 2 *n*-6 and 20 : 4 *n*-6 and increased 18 : 3 *n*-3 content. Flaxseed had minimal effects on 20 : 5 *n*-3 and 22 : 5 *n*-3 content in cattle fed grass hay, but increased 20 : 5 *n*-3 content and led to marginal enrichment of 22 : 5 *n*-3 on the barley-silage diet. Further studies have investigated if echium oil, relatively rich in stearidonic acid (18 : 4 *n*-3), could be used to increase endogenous conversion of C_{18} *n*-3 PUFA to long-chain *n*-3 PUFA[38], since 18 : 3 *n*-3 serves as a substrate for Δ6 catalysed desaturation to 18 : 4 *n*-3 that is considered rate-limiting for the complete desaturation and elongation of 18 : 3 *n*-3 to 20 : 5 *n*-3 and 22 : 6 *n*-3. Supplementing grass-silage with echium oil or linseed oil had no effect on the *n*-6 or *n*-3 PUFA content of beef muscle, but increased the abundance of *trans*-11 18 : 1 and *cis*-9,*trans*-11 CLA. Inclusion of camelina oil or linseed oil have proven effective for increasing 18 : 3 *n*-3 content of IMF in growing sheep, changes that were also accompanied by marginal enrichment of 20 : 5 *n*-3 and 22 : 5 *n*-3 compared with a control diet containing calcium salts of palm oil distillate[43].

The potential of marine sources of PUFA to alter the FA composition of beef has also been investigated. Use of marine algae in combination with either linseed oil or sunflower oil demonstrated that the former elevated 18 : 3 *n*-3 and the latter increased 18 : 2 *n*-6 content[40]. Inclusion of algae with either oilseed increased 22 : 6 *n*-3 content relative to the control, whereas the abundance of 20 : 5 *n*-3 and 22 : 5 *n*-3 were similar among treatments (Table 3). Dietary algae supplements have also been used to enhance long chain *n*-3 PUFA in lamb. In growing sheep, algae rich in 22 : 6 *n*-3 resulted in a marginal decrease in 18 : 3 *n*-3 and dose dependent increases in 20 : 5 *n*-3, 22 : 5 *n*-3 and 22 : 6 *n*-3 content[45]. Changes in maternal nutrition as a mechanism to influence the FA composition of the progeny have been investigated. Nutrition of the dam at mating was found to have minimal effects on lamb FA composition, whereas supplementing the diet of lambs with microalgae increased 22 : 6 *n*-3, and to a lesser extent, 20 : 5 *n*-3 content of *Latissimus dorsi*[44]. The potential of dietary fish oil supplements to alter the FA composition of meat from ruminants has also been examined. Evaluation of different combinations of grass, concentrate and fish oil on lamb FA composition indicated production system (grass or concentrate-based) had a larger influence on overall FA composition than fish oil supplementation, but these findings were based on the feeding of diets with a variable FA content[42]. Concentrate-based diets tended to result in the higher deposition of 18 : 2 *n*-6 in IMF, while fish oil only increased the proportions of 22 : 5 *n*-3 and 22 : 6 *n*-3 when included in the high concentrate diet (Table 4).

Most of the research examining the role of nutrition to alter meat FA composition and content have relied on oilseeds and marine lipid supplements that have two major shortcomings, firstly that the amount of supplemental lipid should not exceed 60 g/kg diet DM without affecting performance and secondly that lipid contained in these supplements is metabolised in the rumen. Feeding rumen protected lipid supplements can, to a certain extent, be used to overcome these constraints[46]. Non-protected and rumen protected sources of linseed and camelina were shown to alter the FA composition of lamb[43]. In unprotected form, camelina oil and linseed oil increased the 18 : 3 *n*-3 content of intramuscular fat with evidence of small increases in 20 : 5 *n*-3 and 22 : 6 *n*-3. Supplements of protected camelina seeds and linseeds resulted in a higher enrichment of 18 : 3 *n*-3 compared with unprotected camelina oil and linseed oil, with sodium hydroxide-treated linseeds resulting in the largest increase in 18 : 3 *n*-3 and long-chain *n*-3 PUFA content (Table 4). Further studies using a rumen protected fish oil supplement indicated 2-fold increase in 18 : 3 *n*-3 and a 4-fold increase in 20 : 5 *n*-3 and 22 : 6 *n*-3 content in *L. thoracis* of growing cattle[47].

Trans fatty acid content of ruminant meat

High intakes of TFA are associated with increased CVD risk and development of insulin resistance[86,87] and increase inflammation[88]. Concerns over TFA consumption and human non-communicable diseases, has lead to nutritional guidelines[6–8], and in some cases legislation[89], recommending a decrease in the TFA content of foods. Such recommendations do not, however, consider differences in the relative abundance and distribution of mono- and polyenoic TFA isomers in ruminant TFA and industrial fats[90], other than distinguishing between isomers of CLA containing a *trans* double bond from other TFA. Enforced or voluntary changes in the refining and processing of plant oils and vegetable fats have decreased the amount of industrial TFA in the human food chain increasing the relative contribution of ruminant TFA to total TFA consumption. Even though there is strong evidence that increases in industrial TFA consumption being associated with mortality from CVD[91], there are insufficient data to conclude on the impact of ruminant TFA intake. Average intake of total TFA in the UK adult population of 0·7 % food energy is below a recommended maximum of 2 % of food energy intake suggesting that present levels of TFA consumption from ruminant foods is not a major CVD risk factor[92].

Ruminant meat contains a range of *trans* 16 : 1 (Δ9–13), *trans* 18 : 1 (Δ4–16) and *trans* 18 : 2 isomers and trace amounts of 18 : 3 containing one or more *trans* double bonds [34–37,93–95]. *Trans* 18 : 1 isomers are quantitatively the most important typically accounting for between 78 and 92 g/100 g total TFA in retail beef and lamb[34–37]. Following absorption, TFA are preferentially deposited in TAG in IMF in contrast to *n*-3 and *n*-6 PUFA that are utilised for the synthesis of phospholipids in muscle membranes[93,95–97]. Isomers of TFA in ruminant meat originate from the rumen formed during

incomplete conversion of dietary unsaturated FA into saturated end products. In cattle and sheep fed high forage diets *trans*-11 18 : 1, an intermediate of 18 : 2 *n*-6 and 18 : 3 *n*-3 metabolism in the rumen is typically the major TFA leaving the rumen[98]. However, high concentrate diets[99], starch-rich low fibre rations containing plant oils[100] or diets supplemented with high amounts of PUFA[84] are known to increase the susceptibility to changes in biohydrogenation pathways favouring the synthesis of *trans*-10 rather than *trans*-11 intermediates. While a low rumen pH and high dietary concentrations of starch and oil can promote the formation of *trans*-10 18 : 1 at the expense of *trans*-11 18 : 1 the underlying causes are not known[98].

Diet has a major influence on the relative abundance of *trans* 18 : 1 isomers in IMF in beef and lamb (Table 5). In cattle and sheep reared on pasture or fed high forage diets *trans*-11 is the major 18 : 1 isomer, whereas *trans*-10 18 : 1 can represent the major TFA in beef or lamb produced on high concentrate diets[34–37,101–103]. Even in animals reared on pasture and conserved grass or forage legumes, deposition of *trans*-10 18 : 1 has been shown to increase during intensive finishing on high concentrate diets (Table 5). Under commercial conditions, the ratio of *trans*-10 18 : 1: *trans*-11 18 : 1 in beef or lamb can vary from low values of 0·1 to as much as 20 depending on diet and management system[17]. Studies in several animal models have provided evidence to suggest that *trans*-10 18 : 1 may have more adverse effects on cardiovascular health compared with *trans*-11 18 : 1[104]. Feeding diets containing plant oils or oilseeds containing *cis*-9 18 : 1, 18 : 2 *n*-6 or 18 : 3 *n*-3 as the major FA can be expected to cause specific enrichment of *trans*-6–8, *trans*-10–12, and *trans*-11–16 in IMF, respectively[90,105,106].

In cattle or sheep fed forages or cereals, total *trans* 18 : 2 abundance in IMF varies between 0·51 and 0·70 g/100 g total FA, concentrations that can be increased to 3·0 g/100 g by dietary supplements of oilseeds or plant oils[39,65,93,107]. Appearance of most *trans* 18:2 in meat originate from ruminal biohydrogenation of C_{18} PUFA, but a proportion of *cis*-9, *trans*-12 18:2 and *cis*-9, *trans*-13 18:2 may also be synthesised endogenously in ruminant tissues[90].

Following the identification of the anti-mutagenic properties of CLA isomers in cooked beef[108–110], numerous studies have investigated the biological activity of isomers of CLA in cell culture and animal models. Much of the research has focused on the effects of *cis*-9, *trans*-11 18 : 2 or *trans*-10, *cis*-12 18 : 2. In addition to the inhibition of mutagenesis, specific isomers of CLA have been demonstrated to modulate energy metabolism, immunity, inflammation, insulin resistance and bone metabolism in several animal models, but evidence that the same physiological effects are also replicated in human subjects remains inconclusive[111–116].

Isomers of CLA are present in a wide range of foods including milk, beef and lamb, and in much smaller amounts (0·1 g/100 g lipid) in pork and poultry[117]. Even though milk and dairy products are the major source in the human diet, lamb, beef and other ruminant meat products contribute to 15–32% of average daily CLA intakes in developed countries[117–119]. Ruminant lipid can contain up to sixteen isomers of CLA with double bonds located at 7,9–13,15 depending on diet and production system. *Cis*-9, *trans*-11 is typically the major isomer due, in the most part, to endogenous synthesis via the action of stearoyl-CoA desaturase on *trans*-11 18:1 that accounts for between 45 and 95% of *cis*-9, *trans*-11 18 : 2 deposited in muscle and adipose of cattle and sheep[98]. Recent studies have also provided evidence that palmitelaidic acid (*trans*-9 16 : 1) may also serve as a substrate for endogenous *cis*-9, *trans*-11 18 : 2 synthesis in ruminant tissues[120]. Most, if not all, of the *trans*-7, *cis*-11 18 : 2 found in ruminant lipid is synthesised endogenously using *trans*-7 18 : 1 as a substrate[98]. Studies in growing lambs and cattle have shown that dietary lipid supplements can be used to enrich *cis*-9, *trans*-11 CLA in muscle up to 2·40 g/100 g FA[15,16], while inclusion of 60 g sunflower oil /kg DM in the diet of Wagyu cattle with a inherently high IMF content resulted in muscle containing 134 mg *cis*-9, *trans*-11 CLA/100 g muscle[121].

Ruminant meat also contain trace amounts of several conjugated linolenic acids that contain at least one conjugated bond[16]. Muscle of growing lambs was reported to contain negligible amounts of *cis*-9, *trans*-11, *cis*-15 18:3, while supplementing the diet with linseed oil over a 42 d finishing period resulting in concentrations of 329 mg/100 g total FA[93]. At finishing muscle in cattle contains between 50–239 and 105 mg/100 g total fatty acid methyl esters (FAME) of *cis*-9, *trans*-11, *cis*-15 18:3 and *cis*-9, *trans*-13, *cis*-15 18:3, respectively, and trace amounts (20 mg/100 g total FAME) of *cis*-9, *trans*-11, *trans*-15 18 : 3[16] Feeding diets containing ground flaxseed over a 140 d finishing period was shown to increase conjugated 18 : 3 content of muscle in beef cows between 30 and 70 mg/100 g total FAME, with evidence that enrichment of specific conjugated linolenic acid isomers is dependent on the composition of the basal diet[39].

Potential to alter meat fatty acid content relative to food labelling claims

Numerous studies have explored the potential to alter meat FA composition, with specific emphasis on elevating *n*-3 PUFA content. It is worth noting altering FA profile has little impact on other aspects of nutrient profile such as protein, vitamins and minerals. The magnitude of increases in *n*-3 PUFA content that can be achieved can be benchmarked against labelling standards established by the European Food Safety Authority. The established standard are based on reference nutrient intakes and recommended daily intakes for adults of 250 mg 20 : 5 *n*-3 plus 22 : 6 *n*-3/d and 2 g 18 : 3 *n*-3/d[122]. Foods should supply >15% of the reference nutrient intakes per 100 g and 418·4 kJ (100 kcal) to be labelled as a 'source of', and >30% of the reference nutrient intakes to be labelled as 'high in'. Meat or meat products must contain ≥40 mg/100 g and per 418·4 kJ (100 kcal) of 20 : 5 *n*-3 plus 22 : 6 *n*-3 or ≥0·3 g/100 g and per

Table 5. Effect of diet on the *trans* 18 : 1 content of beef and lamb (mg/100 g)

Reference	Diet/supplement	Inclusion (g/kg DM)	Wt (kg)	Muscle/ species	Fat (mg/ 100 g)	*Trans* 18:1 isomer										
						Δ4	Δ5	Δ6–8	Δ9	Δ10	Δ11	Δ12	Δ13/14	Δ15	Δ16	Total
Dannenberger *et al.*[96]	Pasture based	–	620	*L. dorsi*	2,300	0·56	0·47	1·94	5·93	6·85	101·7	20·25	37·64	13·94	15·71	205
	Concentrate	–	620	Bovine	2,670	0·57	0·53	2·94	7·84	24·05	66·21	24·99	20·04	7·82	8·22	163
Alfaia *et al.*[103]	Pasture	–	600	*L. lumborum*	1,303	NR	NR	1·17	1·46	1·95	13·18	2·44	NR	NR	3·42*	23·6
	Pasture + 2 mo concentrate	–		Bovine	1,237	NR	NR	1·95	2·98	11·2	13·17	2·75	NR	NR	3·32*	35·4
	Pasture + 4 mo concentrate	–			1,145	NR	NR	1·98	3·22	10·0	13·61	2·97	NR	NR	2·85*	34·6
	Concentrate	–			976	NR	NR	2·48	3·39	15·8	11·99	3·00	NR	NR	2·48*	39·1
Aldai *et al.*[65]	Pasture	–		*L. thoracis*	547	0·10	0·08	0·44	0·87	1·71	14·2	0·74	2·12	0·58	0·78	21·6
	Pasture + 1 mo concentrate	–	516	Bovine	813	0·19	0·22	1·35	1·93	26·2	16·3	1·58	4·04	1·09	1·14	54·0
	Pasture + 2 mo concentrate	–			1,055	0·16	0·18	1·92	3·07	25·4	20·5	1·73	3·93	1·31	1·05	59·3
Juárez *et al.*[107]	Barley	–	562	*L. thoracis*	3,520	NR	NR	9·15	11·6	61·3	22·5	3·87	9·50	7·39	2·11	127
	Ground flaxseed	100†	578	Bovine	4,310	NR	NR	8·19	10·8	33·2	33·6	16·8	42·7	23·3	13·8	1837
Mapiye *et al.*[106]	Red clover silage	–	552	IMF	5,480	NR	NR	5·48	10·4	11·0	60·8	9·32	20·3	12·1	9·86	139
	Rolled flaxseed	150	559	Bovine	6,590	NR	NR	23·7	26·4	33·6	419·8	45·5	92·6	40·2	33·0	712
Bessa *et al.*[93]	Dehydrated Lucerne	–	NR	*L. thoracis*	3,950	0·20	0·40	7·78	8·57	5·81	40·8	8·18	NR	NR	8·18*	79·9
	Sunflower oil	74	NR	Ovine	4,500	1·53	2·12	16·6	20·3	24·9	214	29·7	NR	NR	29·7*	339
	Sunflower oil + Linseed oil	37 + 37	NR		5,710	1·66	2·63	21·9	24·0	25·7	300	35·2	NR	NR	35·2*	446
	Linseed oil	74	NR		4,920	1·38	1·82	16·3	18·7	14·8	201	27·3	NR	NR	27·3*	309
Meale *et al.*[45]	Barley + Lucerne hay	–	43·0	Skirt	NR	NR	NR	31·4	34·3	228	384	NR	NR	NR	NR	NR
	Marine microalgae	10	46·1	Ovine	NR	NR	NR	16·0	23·6	189	496	NR	NR	NR	NR	NR
	Marine microalgae	20	44·3		NR	NR	NR	13·4	17·6	156	313	NR	NR	NR	NR	NR
	Marine microalgae	30	45·0		NR	NR	NR	17·9	19·4	111	265	NR	NR	NR	NR	NR

IMF, intramuscular fat; NR, not reported.
* Elutes with the same retention time as *cis*-14 18 : 1 during gas-chromatography analysis.
† Inclusion rate g/kg as fed.

418·4 kJ (100 kcal) 18 : 3 *n*-3 to be labelled as a 'source of' *n*-3 PUFA; or ≥80 mg 20 : 5 *n*-3 plus 22 : 6 *n*-3 per 100 g and 418·4 kJ (100 kcal) or ≥0·6 g per 100 g and per 418·4 kJ (100 kcal) 18 : 3 *n*-3 to be labelled as 'high in' *n*-3 PUFA[123]. When interpreting data reported in the literature, *n*-3 PUFA enrichment is typically reported on a mg/100 g basis, and often the energy content of meat or meat products has not been determined.

Based on amounts of FA (mg/100 g) in muscle for pigs (Table 1) and chickens (Table 2) reared on diets containing linseed or flaxseed it is possible to enrich 18 : 3 *n*-3 above 0·3 g/100 g. For pigs fed high amounts of flaxseed it is possible to increase 18 : 3 *n*-3 in pork to 615 mg/100 g[32], a concentration that exceeds the threshold for a 'high in' *n*-3 PUFA claim. At the same time, the increases in muscle total fat content and associated enrichment of 20 : 5 *n*-3 plus 22 : 6 *n*-3 also results in pork meeting the requirements for a 'source of ' long-chain *n*-3 PUFA[32]. Feeding dietary supplements of fish oil to pigs has also been shown to increase the 20 : 5 *n*-3 and 22 : 6 *n*-3 content of pork to levels required to meet the 'source of' claim[28]. Use of fish oil or marine algae can also be used to increase the combined amount of 20 : 5 *n*-3 and 22 : 6 *n*-3 in chicken to levels above 80 mg/100 g[22,24,25]. It is also possible to enrich 20 : 5 *n*-3 plus 22 : 6 *n*-3 in muscle to meet the 'high in long chain *n*-3 PUFA' by feeding broilers diets containing flaxseed oil for at least 21 d[26]and exploiting endogenous conversion of 18 : 3 *n*-3 to 20 : 5 *n*-3 and 22 : 6 *n*-3 in avian muscle.

All the studies outlined in Tables 3 and 4 relating to beef and lamb fail to meet the required ≥0·3 g of α-linolenic acid to even be classed as a 'source of' *n*-3 PUFA. Moreover, the highest 18 : 3 *n*-3 content for beef was 71·7 mg/100 g in the study by Nassu *et al.*[39] when feeding grass hay and flaxseed. For lamb, the highest 18 : 3 *n*-3 content was 125·5 mg/100 g with Uruguayan grass-finished heavy lambs[62]. Nevertheless, some studies did achieve adequate levels of EPA plus DHA to meet 'a source of' and 'high in' claims. Feeding 275 g/d of protected fish oil resulted in 67·7 mg/100 g of EPA plus DHA in beef, satisfying 'a source of' *n*-3 PUFA' claim[122]. Equally, Annett *et al*[42] achieved 52·5 mg/100 g EPA plus DHA in lamb fed a fish oil enriched concentrate. Microalgae supplementation of lamb has also been successful in sufficiently increasing EPA plus DHA levels to allow *n*-3 PUFA health claims. Supplementing diets with 1 and 2% DM microalgae achieved 'a source of' levels of EPA plus DHA (59·1 mg/100 g and 75·9 mg/100 g, respectively), while 3% DM supplementation achieved 146·1 mg/100 g EPA plus DHA, which is sufficient to claim 'high in' *n*-3 PUFA[45]. Both control treatments in the study by Hopkins *et al*[44] attained 'a source of' levels of EPA plus DHA while supplementing these diets with microalgae increase EPA plus DHA levels to above 'high in' levels.

While it is helpful to be able to compare relative to labelling standards of European Food Safety Authority, it would be much more useful to assess the relative nutritional value through human intervention studies. There is a distinct lack of this approach in the literature.

Conclusions

Meat provides a range of macro and micronutrients for man. The nutritional value of meat is an important factor influencing consumer preferences for various white and red meats. Substantial progress has been made on reducing the fat content of meat and much effort has focused on approaches for improving FA profile with much emphasis on *n*-3. Pork and chicken may be enriched with long-chain *n*-3 by inclusion of fish oil or microalgae in the diet. Enrichment of beef and lamb is more challenging due to the extensive lipolysis and biohydrogenation of dietary lipids by the rumen microbiome. However, some studies have achieved high levels of long-chain *n*-3 in lamb, sufficient to be noted as high-in *n*-3 FA according to the guidelines by the European Food Safety Authority. Despite all the efforts to improve lipid profile of meat there is a distinct lack of studies examining the impact through human intervention studies. This essentially helps to make better judgments on the impact of nutritional value on human health and well-being.

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Conflicts of Interest

None.

Authorship

All authors contributed to the review of published reports. E. M. P., S. A. M. and K. J. S. performed searches of published literature and prepared the Tables summarising information on meat fat composition. All authors reviewed the manuscript contents. N. D. S., S. A. H. and K. J. S. were responsible for the final manuscript contents.

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